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Climbing Collembola

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With 7 figures

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1. Introduction

Collembola usually form a major part of the fauna of the upper layers of soil and the soil surface. The expressions "vertical migration" and "vertical distribution" are often used to describe movement and distribution of Collembola in the soil profile, but there has been no previous indication that comparable movements or distribution could be found above the surface, although certain observations — e.g. that several species of Collembola are found as pollen feeders in flowers (KEVAN and KEVAN 1970) — pre-suppose movement upwards from the ground.

During routine sorting at Rothamsted of catches from light traps, the entrances of which are a distance above ground level, Collembola were noticed on many occasions, sometimes in large numbers. We report some observations on this and related topics. Although the work was ad hoc, carried out as and when possible, the results are nevertheless coherent and reveal an interesting aspect, not apparently previously recorded, of the biology of some Collembola.

2. Methods

2.1. Light traps

Four Rothamsted light traps (WILLIAMS 1948) are sited at Rothamsted Experimental Station as part of the Rothamsted Insect Survey (TAYLOR 1973). The light source is a 200-watt clear tungsten bulb, opposite the trap entrance at a height of 1.2 m above ground level. The light bulb is inside a tetra-hedral glass cover, and the trap has a flat, metal roof.

A killing agent, tetrachlorethane, is used in all these light traps. Traps are operated on a time-switch set to switch on half an hour after sunset and before sunrise (local time) and the traps are operated every night. They are emptied every day at 10.00 hr; Collembola were extracted from catches within an hour or two of collection from the trap site. Identification was in some cases done immediately; other catches were preserved in 70% alcohol for later examination, but some of the earliest catches were stored dry and then soaked in an alcohol/glycerol mixture overnight before examination.

Some live samples were collected from the framework of the light traps by means of an artist type brush dipped in an alcohol/glycerol mixture, in which specimens so collected were stored.

2.2. Sticky traps

Grease bands (PBI Boltac Medium Size) were placed at a height of 1 m on the legs of the woodland traps (see below) and removed for examination after one week. Similar bands were placed on mature ash trees, with clear boles, at heights of 2 m, 4.07 m, 4.86 m, 5.02 m and 5.28 m. These tree bands were in place for 3 days at 2 m (17—19 August 1974) and 5 days at the other heights (11.—16. September 1974). All sticky bands were, after removal from trap legs or trees, placed between cellulose-acetate sheets to permit storage and subsequent examination.

2.3. Pitfall traps

Three pitfall traps, each a 7 cm diameter glass jar containing an alcohol/glycerol mixture, were sited during August 1974 near the woodland light traps, two at distances of 2 m and 5 m from one trap, the third 3 m from the other trap. Initially they were uncovered but a 2 mm mesh grid was later placed over each to stop access to larger insects.

2.4. Meteorological data

Daily records are maintained at a meteorological site about 450 m north of the major sites in woodland and 250 m to 350 m south of the other two light trap sites. Air temperatures are recorded in a standard Stevenson screen and rainfall in a 5-inch diameter gauge.

2.5. Sites

Most of the observations refer to two traps sited about 50 m. apart in Geescroft Wilderness at Rothamsted. These traps are designated GI and GII. Geescroft Wilderness is a small (1.2 ha) deciduous woodland, left undisturbed since 1867, in which vegetation, briefly described by THURSTON (1960), is chiefly elm, ash and oak with a sparse understorey and little ground cover near the trap sites except for a shallow (2.5–5.0 cm.) layer of leaf litter. The soil is a leached brown flinty silt loam over clay-with-flints, described by EDWARDS and HEATH (1963).

The other two trap sites are both in open situations. The Allotments trap (A) is sited in a completely exposed area which, at the time of the observations, was a recently levelled bare spoil tip, chiefly of clayey sub-soil. The Barnfield trap (B) is sited on a grassed path flanked to the west by a hard tennis court and to the east by an arable field which, in 1973, was sown to field beans (*Vicia faba*).

3. Results

3.1. Method of entry to light traps

Since the entrance to the Rothamsted light trap is 1.2 m above ground level, Collembola could have been blown in by wind. In that event, enormous numbers would have been airborne on occasion. To test this possibility, the legs of the traps were sticky-banded in March 1973. Numerous Collembola were trapped, listed in table 1, and the majority of these were on the lower edges of the bands, as shown in fig. 1A and 1B. Further, there were no Collembola in the light trap used for the experiment (GI) while the legs were banded, but on

Table 1. Collembola collected on sticky bands, GI

Species	Number
<i>Entomobrya nivalis</i> (L.)	23
<i>Entomobrya albocincta</i> (TEMPLETON)	2
<i>Orchesella cincta</i> (L.)	1
<i>Isotoma arborea</i> (L.)	10
Dicyrtomid Gen. sp.	56
	<u>92</u>

Bands in place 8.—14. March 1973.

removal of the bands Collembola were again trapped. As a confirmatory test, bamboo poles were sited at several places close to the light traps and sticky banded at various heights. Although numerous flying insects were trapped, there were no Collembola on any of the

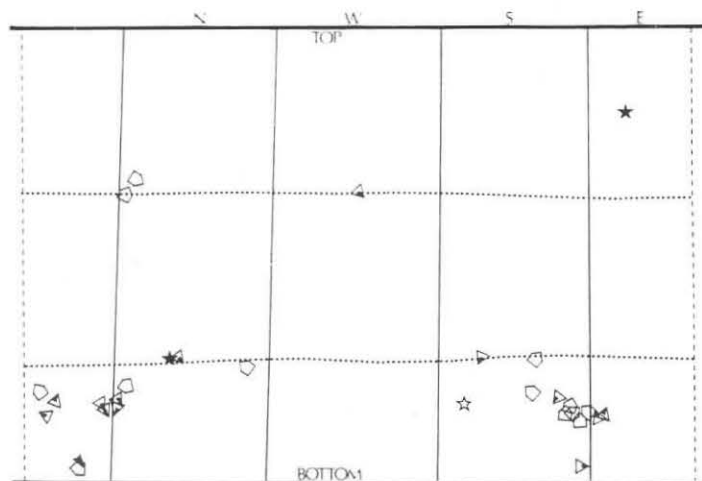
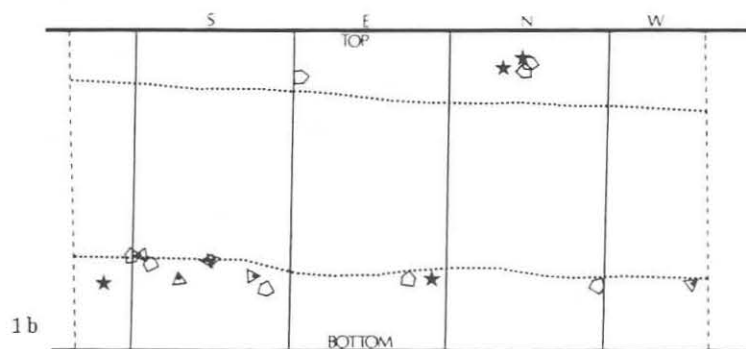


Fig. 1. Diagrams of sticky bands from legs of GI light trap, showing division into top, middle and bottom segments.

◻ = Entomobryidae; ▲ = Sminthuridae
 ★ = Isotomidae; ☆ = Poduridae

Arrow head, for Entomobryidae and arrow head in symbol for Sminthuridae, indicates direction of head of animal.



bamboo sticky bands, including the lower margins. This latter observation was expected since it was anticipated that the smooth, clean surface of the bamboo would prevent Collembola climbing the poles.

From these results, the wind borne hypothesis was discarded; Collembola were found in the light traps because they were climbing the legs.

3.2. Effect of light source

A 200-watt tungsten bulb is not merely a light source; i.e. emitting energy within the visible part of the electromagnetic spectrum. It also emits, for instance, at infra-red wavelengths and, as a heat source, could possibly create a temperature gradient between the ground and trap height. Therefore the light source could, for one reason or another, cause Collembola to be trapped. During the period 4./5. to 8./9. August 1973, inclusive, the bulb in GI failed and was not replaced. Table 2 shows the species and numbers of Collembola recorded in GI in the 120 h approximately without a light source. Obviously, the light source did not cause Collembola to climb.

Table 2. Collembola Collected in Trap GI, 4.—5. to 8.—9. August 1973; trap without light source

Species	Number
<i>Entomobrya nivalis</i>	52
<i>Entomobrya albocincta</i>	8
<i>Orchesella cincta</i>	263
<i>Tomocerus minor</i> (LUBBOCK)	4
<i>Pseudachorutes asigillatus</i> (TULLBERG)	47
<i>Isotoma arborea</i>	7
Total	<u>381</u>

3.3. Time of activity

Between 12. and 16. March 1974, inclusive, the trap receptacle of GI was changed twice in each 24 h period, at 10.00 h and 17.00 h, local time. Although not a precise light/dark separation, table 3 shows that most climbing occurs between 17.00 h and 10.00 h, including that of *Entomobrya nivalis*. Joosse (1965) showed that a lot of surface activity occurred at night, but found that *E. nivalis* was most active during the day.

Table 3. Numbers of Collembola collected in GI between 10.00 hr and 17.00 hr and between 17.00 hr and 10.00 hr

	10.00—17.00	17.00—10.00
Total	<u>12</u>	<u>34</u>
<i>Entomobrya nivalis</i>	<u>7</u>	<u>27</u>

3.4. Species trapped and periods of activity

A summary of captures for various dates in 1972, 1973 and 1974 is given in tables 4, 5 and 6. Ten species have been found, the commonest being *Entomobrya nivalis* and *Orchesella cincta*, with *Tomocerus minor* and *Isotoma arborea* frequent and occasionally present in large numbers. The tables show that climbing can occur at any time of year and that low temperatures are not inhibitory. The largest single catch of *I. arborea*, of over 100, occurred at an air minimum temperature of -3.7°C and a grass minimum of -8.9°C , and quite

Table 4. Collembola in Traps GI and GII

Date	GI			GII			Notes		
5./6. III. 1972	O		E*		I				
9./10. IX. 1972	O	T	E	P	I				
10./11. IX. 1972	O	T	E	P		O	T	E	
10./11. X. 1972	O**	T	E**	P	I**	D	O**	T	E** I**
10./11. XI. 1972	O**	T	E**		I**				
14./15. XI. 1972	O		E		I				Air Min. Temp. —1.5 °C; Grass min. temp. —5.2 °C
19./20. XI. 1972	O		E		I				Grass min. temp. +0.1 °C
20./21. XI. 1972	O		E		I				Grass min. temp. +1.0 °C
30. XI./1. XII. 72	O*		E*		I				
7./8. XII. 1972	O*		E*		I				
19./20. XII. 1972	O*		E*						
15./16. I. 1973	O*		E*	P	I				Air min. temp. —1.9 °C; grass min. temp. —5.4 °C
8./9. II. 1973	O		E**	P	I	D*			
19./20. II. 1973	O		E*		I				
29./30. XI. 1973						E	I***		Air min. temp. —3.7 °C; grass min. temp. —8.9 °C

(O) *Orchesella cincta*, (T) *Tomocerus* sp., (E) *Entomobrya nivalis* — *albocincta*, (P) *Pseudachorutes asigillatus*, (I) *Isotoma arborea*, (Du) *Dicyrtomina* sp.

No asterisk) Number 1—10; (*) 10—50; (**) 50—100; (***) >100 ; (blank) no record.

Table 5. Collembola from Rothamsted light traps

Light Trap	Date	<i>E. nivalis</i>	<i>E. albocincta</i>	<i>E. multifasciata</i> TULLBERG	<i>O. cincta</i>	<i>T. minor</i>	<i>T. longicornis</i>	<i>S. fuscus</i> L.	<i>I. arborea</i>	<i>P. aspillatus</i>	<i>L. cyanus</i>	Total
A	21./22. IX. 1973	—	—	95								95
B	22./23. IX. 1973	—	—	68								68
B	20./21. VIII. 1974	—	—	2								2
B	22./23. VIII. 1974	—	—	4								4
A	24./25. VIII. 1974	—	—	3	—	—	—	—	—	—	1	4
GI	30./31. I. 1972	16	4	—	11	—	—	—	—	—	—	31
GI	19./20. VII. 1972	25	—	—	30	—	—	—	—	—	—	55
GI	12./13. III. 1973	11	2	—	1	—	—	—	—	—	—	14
GI	30. IV./1. V. 1973	50	2	—	3	—	—	—	—	—	5	60
GI	8./9. XI. 1973	12	1	—	8	—	—	14	2	6	—	43
GI	13./14. III. 1974	4	—	—	—	—	—	—	—	—	—	4
GI	14./15. III. 1974	3	—	—	—	—	—	—	—	—	—	3
GI	15./16. III. 1974	2	—	—	—	—	—	—	—	—	—	2
GII	9./10. VI. 1974	10	1	—	—	—	—	—	—	—	—	11
GII	12./13. III. 1974	4	—	—	—	—	—	—	—	1	2	7
GII	13./14. III. 1974	7	—	—	—	—	—	—	2	—	—	9
GII	14./15. III. 1974	3	1	—	—	—	—	—	—	—	—	4
GII	15./16. III. 1974	3	—	—	1	1	—	—	1	—	2	8
GII	25./26. IV. 1974	13	—	—	—	2	—	—	—	2	—	17
GII	27./28. IV. 1974	7	—	—	—	—	1	—	—	—	—	8
GII	26./27. VI. 1974	38	1	—	27	65	1	—	—	4	—	136

A = Allotments Light trap, B = Barnfield Light trap, GI = Geescroft I, GII = Geescroft II

Table 6. Species and numbers of Collembola from traps GI and GII, August 1974

Species	GI	GII	Total
<i>Entomobrya nivalis</i>	54	192	246
<i>Entomobrya albocincta</i>	19	14	33
<i>Orchesella cincta</i>	252	256	508
<i>Tomocerus minor</i>	8	119	127
<i>Tomocerus longicornis</i> (MÜLLER)	0	33	33
<i>Pseudoscorpiones aspillatus</i>	7	4	11
* <i>Sminthurus fuscus</i>	4	248	252
	344	866	1210

* All specimens of *S. fuscus* on outside of traps.

substantial catches of other species of Collembola occurred when air and ground temperatures were below 0 °C (table 4).

Table 5 suggests that there is, at Rothamsted, a distinct habitat separation between *Entomobrya nivalis* and *E. albocincta*, occurring in woodland, and *E. multifasciata* in open habitats. Although little attention was paid to the traps in the open situations, the separation is supported by the fact that, of many hundreds of specimens of *Entomobrya* examined from the woodland traps, none were identified as *E. multifasciata*.

Sminthurus fuscus requires some comment. The large number recorded from GII in August 1974 (table 6) were from the outside of the trap. It occurred in small numbers on another occasion in GI (table 5) but it was common on the traps, particularly on the flat metal roof. It is not known why this species, in contrast to the others, did not enter the traps but it is possible that the light source was inhibitory. That *S. fuscus* can climb sloping glass was proved by its capture in a replica of the tetra-hedral glass cover which was placed,

on a board, on the surface litter. However, *S. fuscus* was inactive during the day when on the traps, except that it jumped when disturbed, and when laboratory cultures were placed in the bright light from a window activity stopped. The trap light source is a bright one (approximately 2700 lumens) so when the glass exterior, close to the bulb, was reached further movement may have been inhibited. Other species, particularly *Entomobrya* spp., were found on the outside of the traps but, as is evident, also entered the traps in large numbers, so presumably have a different reaction to light. The data for *S. fuscus* are qualitative, its' jumping ability making it difficult to capture all specimens on the traps. The numbers recorded do show that large numbers of *S. fuscus* will climb up from the soil surface and also suggest considerable differences in the microhabitats around the woodland traps, but they are not a quantitative sample of populations.

3.4. Relation of catch to rainfall

Casual observation suggested that numbers caught increased after rain. The results of a study made in August 1974 are shown in fig. 2. Clearly, most Collembola were caught in the traps when it rained, particularly in the 24 h following a substantial fall. This relationship is confirmed in the catches made in August 1973 in trap GI, fig. 3, and by the data from the pit-fall traps in August 1974, fig. 4. The catches recorded on 4. August 1974 are an exception to the general occurrence of larger catches after rain; these catches coincided with rain, but the large fall of 4. August was the first notable rain after a period of well over a week without significant rain. There is a very poor correlation between 24 h catches

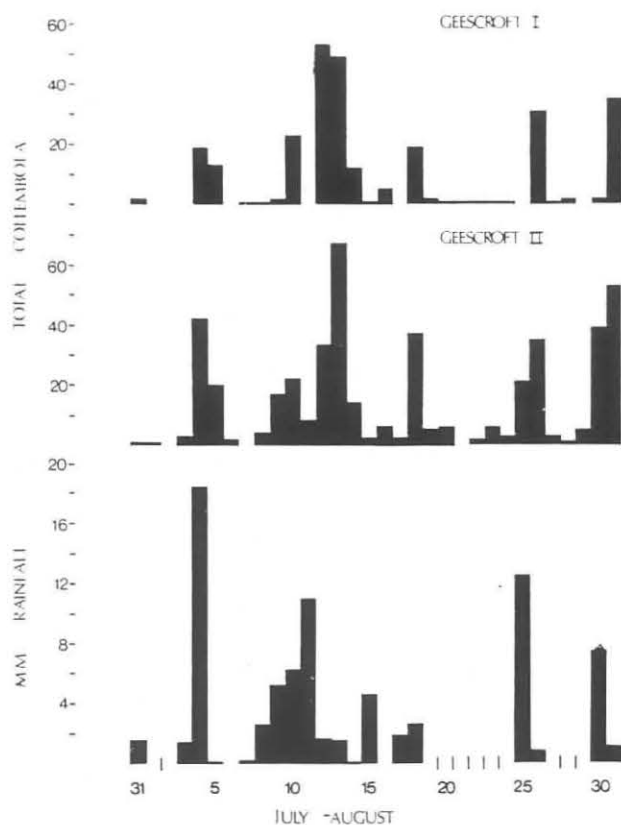


Fig. 2. Daily totals of rainfall and numbers of Collembola in GI and GII light traps, 31. July to 31. August 1974.

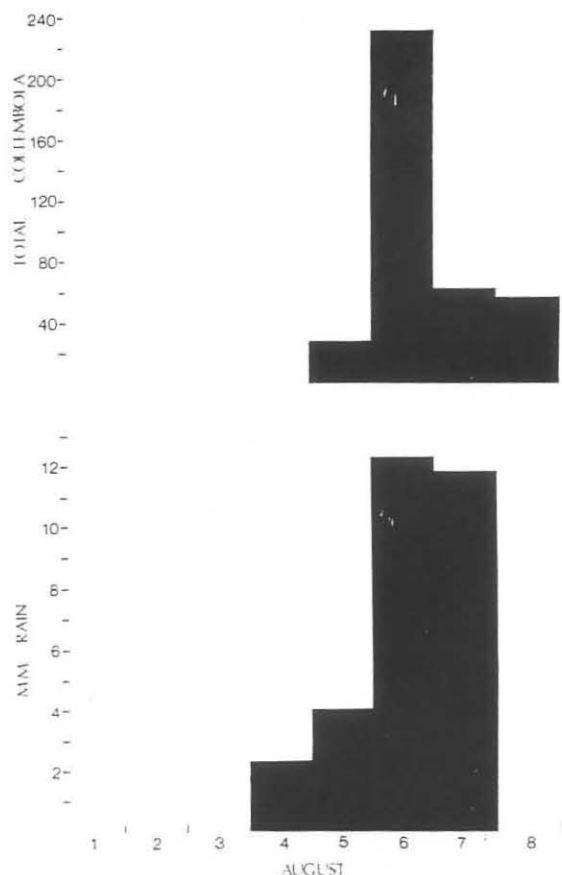


Fig. 3. Daily totals of rainfall and numbers of Collembola in G1 light trap, 1. to 8. August 1973.

and rainfall of the same or the preceding day, but it is evident from fig. 2 that there are distinct periods of rain alternating with dry days. If these rain spells are considered as separate "rain events", there is a very high correlation between catch and rainfall per "event", as shown in figs. 5 and 6. The catches of the light-less week of August 1973 have been included as, fortuitously, they coincided with a "rain event". The data thus strongly suggest an exponential relationship between rainfall and the amount of climbing activity by Collembola, for individual species as well as all species combined. *Entomobrya nivalis* and *Orchesella cincta* were the commonest species; as shown in fig. 6, the rate of increase in numbers of *O. cincta* climbing is greater than that of *E. nivalis*. All three regressions have an intercept of almost zero, which is additional evidence that rainfall is the direct cause of climbing in Collembola.

3.5. Vertical distribution

The numbers and species trapped on tree trunks are shown in tables 7 and 8. Species composition and relative abundance are comparable to those at 1 m. and the species are also those taken in the light traps. The position of the majority of the individuals, figs. 7, A, B, show that, as at lower levels, most movement is upwards.

The sticky bands were of different lengths and were in position for different periods at different times. The trap legs are 5×5 cm; the tree trunks varied in circumference at band

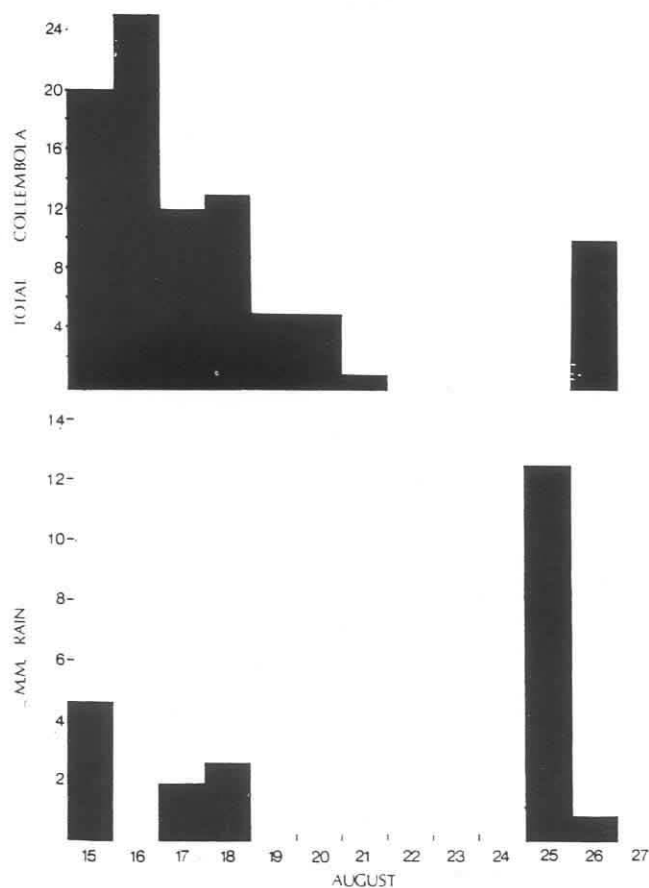


Fig. 4. Daily totals of rainfall and numbers of Collembola in 3 pitfall traps, Geescroft, 15. to 27. August 1974.

Table 7. Species of Collembola and positions on sticky band at height of 2 m

Species	Lower edge	Middle and under band	Upper edge	Total
<i>Entomobrya nivalis</i>	11	0	3	14
<i>Entomobrya albocincta</i>	0	1	0	1
<i>Orchesella cincta</i>	14	1	4	19
<i>Tomocerus minor</i>	14	0	1	15
<i>Sminthurus fuscus</i>	2	2	1	5
Unidentifiable	3	1	0	4
Total	44	5	9	58

height from about 75 cm to 100 cm and the bands were in place for 7 days on the light traps, 3 days at 2 m and 5 days at the other heights. A rough comparison can be made by reducing catches to individuals per 5 cm length per day and table 9 gives the result of this standardisation. The result suggests that there are as many individuals at 2 m as at 1 m, and while catches at greater heights are variable, substantial numbers do occur. The average catch at 4—5 m (average for these heights 4.81 m) is 0.17/5 cm/day, a ratio of about 1:5 to catch at 1 m.

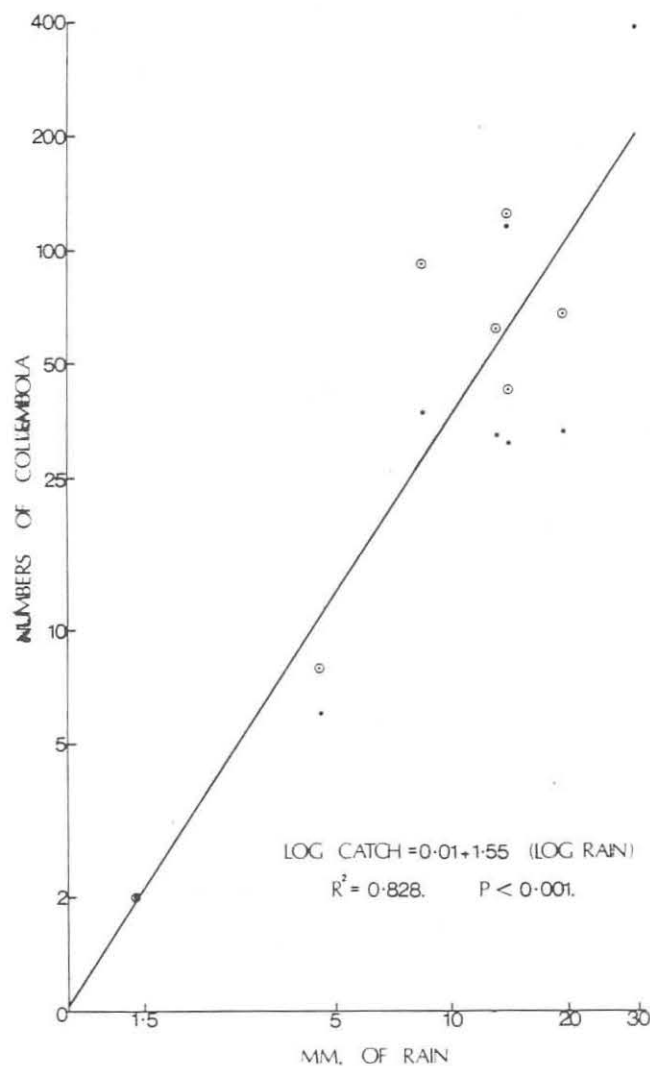


Fig. 5. Relation between amount of rainfall per rainfall event and corresponding totals of Collembola in GI and GII light traps, ● = GI; ○ = GII.

4. Discussion

We have shown that large scale movements above ground level occur regularly in several species of Collembola, which appear to be a significant feature of the biology of at least some of the species involved. HÖREGOTT (1960) recorded Collembola in tree-tops and they are commonly found on vegetation as well as bark, the epigeon and xeromorph life forms of CHRISTIANSEN (1964). This author remarks that little work has been done on the vertical distribution of epigeon populations and our results show that such work would shed much new light on Collembola biology.

Rainfall seems to be intimately connected with climbing and the data we present are the most precise relationship yet established between rainfall and activity of Collembola. Previous work has been rather contradictory; for example, PEDIGO (1970) showed that rainfall increased activity of surface woodland Collembola, a conclusion amply confirmed

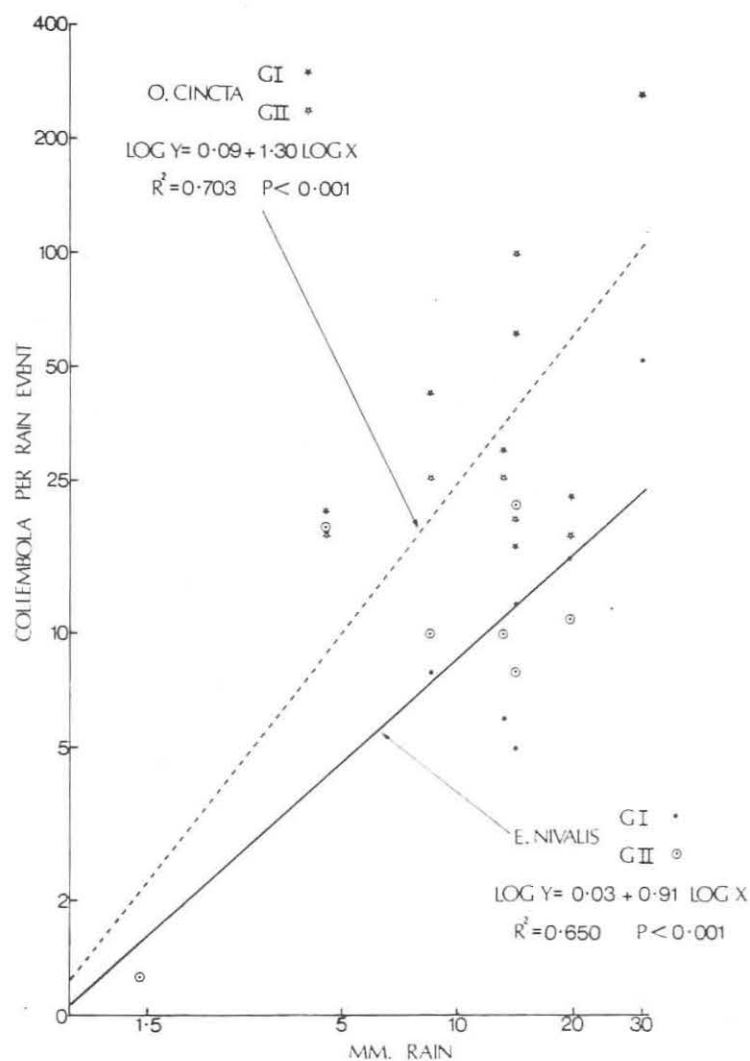


Fig. 6. Relation between amount of rainfall per rainfall event and corresponding catches of *Entomobrya nivalis* and *Orchesella cineta* in GI and GII light traps.

by our own data, but Joosse (1965) stated that occasional showers did not affect activity. However, pitfall traps, as used by these and other workers, reflect only horizontal surface movement, and this movement is, under the influence of rainfall, transformed into, or is concomitant with, upward movement not detected by pitfall traps. The mechanisms causing upward movement are obscure, although some suggestions can be made.

GRIFFITHS and BIRCH (1961) showed that CO_2 concentrations in the soil increased after rain and SOUTH (1961) noted that CO_2 has an anaesthetic effect on Collembola. MOURSI (1962) found that activity of mites was affected by changes in concentrations of gases, particularly in the oxygen content. It is possible, therefore, that Collembola react to changes in either the absolute or the relative concentrations of gases in surface litter resulting from changes in microbiological activity consequent on rainfall. Or, alternatively, they are driven out of macropores by ingress of water.

Table 8. Species of Collembola and positions on bands at heights of 4–5 m

Species	Lower Edge			Middle/under band					Upper Edge			Totals	
	4.07 m	4.86 m	5.02 m	5.28 m	4.07 m	4.86 m	5.02 m	5.28 m	4.07 m	4.86 m	5.02 m		5.28 m
<i>Eutomobrya nividis</i>	1	0	18	5	0	0	3	2	2	2	0	1	34
<i>Eutomobrya albocincta</i>	0	2	8	0	0	0	0	0	0	0	0	0	10
<i>Orchesella cincta</i>	0	2	1	0	0	2	0	0	0	0	0	0	5
<i>Tomocerus minor</i>	0	0	2	0	0	0	0	0	0	0	0	0	2
Unidentifiable	0	0	0	2	0	0	0	0	0	0	0	1	3
	1	4	29	7	0	2	3	2	2	2	0	2	54
	41			7					6				

UETZ (1974) showed that rain flattens leaf litter, or, that cavity size is reduced. Cavity size is important in determining vertical distribution within the soil profile (CHRISTIANSEN 1964, WALLWORK 1970) and the reduction in cavity size caused by rainfall — and, presumably, the heavier the rain the greater the reduction — could account for vacuation of the litter layer and also the relationship between numbers and rainfall — figs. 5 and 6.

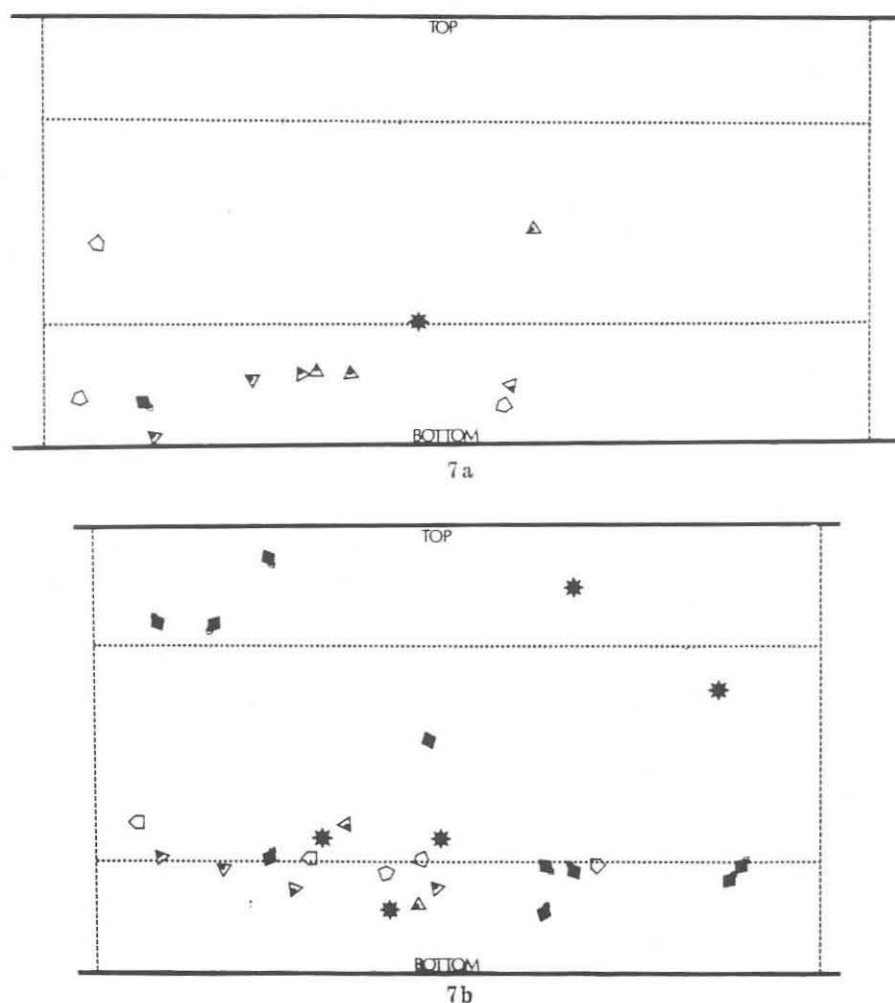


Fig. 7. Diagrams of consecutive segments of sticky band on tree at 5.02 m, showing division into top, middle and bottom sections used in tables 7 and 8.

◻ = *Entomobrya nivalis*;

△ = *E. albocincta*;

◆ = *Orchesella cincta*;

★ = Unidentifiable.

Arrow heads, for *E. nivalis*, *E. albocincta* and *O. cincta* indicate direction of head of animal.

Table 9. Comparison, as individuals per 5 cm length of band per day, of catches at different heights and proportionate catch with catch at 1 m = 100

Height in m	Individuals per 5 cm per day	Catch ratio 1 m = 100
1.00	0.9	100
2.00	1.1	122
4.07	0.04	4
4.86	0.1	11
5.02	0.4	45
5.28	0.12	13

However, these suggestions merely indicate mechanisms which might cause Collembola to leave the litter layer; they do not explain why such large numbers should climb up to 5 m, or why even larger numbers should be found at 1 m and 2 m. The frequency and regularity of, and the numbers both of species and individuals involved in climbing, suggest that some advantage is gained by this activity and that it is not merely vacation of a normal habitat which has become temporarily unsuitable. The advantages, if they exist, are not obvious.

There seems to be an association between epiphytic growth and climbing. Larger numbers were trapped on the southwest and northwest legs of G1, which had dense algal growth, than on the southeast and northeast legs which had sparse growth. Trap GII was installed in early 1973 and did not develop algal growth until 1974; very few Collembola were found in GII in 1973 whereas in 1974 large numbers occurred. Such differences in potential food sources could account for differences in numbers between different types of "trunks", either directly or indirectly because of a more favourable microclimate and may thus also cause some selection of climbing routes. But they too do not account for the frequency, regularity and scale of movement upwards.

A further possibility is that climbing increases the chances of dispersal. BERLAND (1934, 1935, 1936), GLICK (1939) and FREEMAN (1952) report Collembola in the air at heights up to 2,000 m (BERLAND) and 3,350 m (11,000 ft.) (GLICK). DELAMARE-DEBOUTTEVILLE (1951) showed that *Sminthurus malmgreni* was dispersed by strong winds and POOLE (1961) showed that gales caused changes in species composition of woodland populations of Collembola. BUAHIN (1965), using water traps and suction traps, showed that Collembola were frequently trapped over grass at heights up to 122 cm, and estimated that relative density at 122 cm was about half that at 2.5 cm in three species. The profile of *Entomobrya multifasciata* was comparatively flat and statistically non-significant, the relative density at 122 cm being about 75% of that at 2.5 cm. BUAHIN considered that aerial dispersal played an important role in dispersal of Collembola and their ability to colonise new habitats rapidly, a conclusion of some interest in view of the large numbers of *E. multifasciata* taken in the Allotments trap (table 5) when it was standing on bare, clayey subsoil. Climbing will enable Collembola to launch themselves, or to be launched, into moving air, but woodland would not seem to be an entirely suitable take-off site and neither does a distributive function seem apposite to climbing in air temperatures several degrees below freezing.

We have little information on the composition of Collembola populations in the litter layer over which the traps stand. A few samples taken (for other purposes) in March 1974 contained *Orchesella cincta*, *Tomocerus* sp., *Dicyrtomina* sp., and a large species of *Isotoma* not found in the light traps; rather surprisingly, no *Entomobrya* were found. The pitfall trapping done simultaneously with banding in August 1974 showed that the climbing species were also present, in large numbers, in the litter layer. One would anticipate some relationship between arboreal populations and those on the ground, which are, presumably, the source of arboreal populations. One must otherwise assume a large, permanent arboreal fauna, of many species, which regularly moves between trees. This, however, implies movement down trunks on the same scale as movement up, and none of our evidence suggests that there is any significant downward movement. This is of particular interest with regard

to *Isotoma arborea*, which one would not expect to find on the ground. Yet, as is evident from table 4, this species must occur on the ground, sometimes in large numbers, to account for its presence in the light traps.

Pitfall traps, which record horizontal movement at the surface, are commonly used to estimate activity and distribution of Collembola, but they will obviously not detect movement upwards from the ground. Additional techniques, such as the use above the surface of, for example, water traps, sticky traps or suction traps are thus essential for proper monitoring of changes of activity, numbers and distribution of Collembola. Vertical movements above the ground are not restricted to Collembola. Mites, particularly predatory Prostigmata and especially Trombidid nymphs, Diplopoda and Chilopoda were all found on the tree bands at 4 m and 5 m, and Trombidid nymphs, Diplopoda, Chelonethida and Isopoda are frequently found in the Geescroft light traps, although the Chelonethids may be there because of phoresy. Sampling methods which do not allow for climbing, by many taxa hitherto assumed to be largely if not exclusively of surface or sub-surface habitat, will not reveal the behaviour we have demonstrated. Depending on the importance of climbing in the ethology and ecology of an animal, there will be larger or smaller lacunae in data, and interpretations thereby vitiated, unless above-ground sampling becomes an integral part of investigations on these animals.

5. Summary · Résumé

The work described was done at Rothamsted Experimental Station in south-east England, mainly in an established, mixed deciduous wood.

Ten species of Collembola were found to occur in light traps, which were raised on legs with the trap opening 1.2 m above ground level. Sticky bands on the legs of the traps stopped catches. Large numbers were taken when the light of one trap was inoperative, showing that Collembola were not attracted by the light source although much of the climbing seemed to occur at night.

Climbing occurs at all times of year and large catches were recorded with air and ground temperatures well below 0 °C.

Climbing is directly related to rainfall. An exponential relation was found between amount of rainfall and numbers in light traps, for total numbers caught and for numbers of the two commonest species, *Entomobrya nivalis* and *Orchesella cincta*.

Tree banding showed that Collembola climbed up to at least 5 m, at which level about one fifth as many occurred as at 1 m and 2 m: at these levels numbers were about equal.

No satisfactory explanation can be advanced for this activity, which takes place often and on a large scale. Changes in gaseous concentrations in the leaf litter, or compaction following rain, may cause vacation of the leaf litter layer but do not explain climbing. There may be an increased chance of aerial distribution but this may not be relevant to normally arboreal species such as *Isotoma arborea* which, it is shown, must on occasion occur in large numbers on the ground.

It is stressed that large scale movement upwards from ground level will not be reflected in pitfall traps, so that additional techniques such as water traps, sticky traps or suction traps, above ground level, are essential for proper monitoring of changes of activity, numbers and distribution of Collembola.

Des Collemboles grimpeurs

Ce travail fut réalisé à la station expérimentale de Rothamsted, située au sud-est de l'Angleterre principalement dans une forêt feuillue mélangée.

A l'aide de pièges lumineux montés sur pied à 1.2 m au-dessus du sol dix espèces de Collemboles ont été mises en évidence. Les captures sont arrêtées lorsque des bandelettes adhésives sont fixées aux pieds des pièges. Un grand nombre de Collemboles ont été récoltés lorsque la lumière d'un des pièges était éteinte. Ceci montre que les Collemboles n'étaient pas attirés par la source de lumière bien que l'ascension ait lieu en grande partie durant la nuit.

L'escalade se produit à n'importe quelle époque de l'année. D'importantes récoltes ont été obtenues lorsque la température de l'air et celle du sol descendaient bien en dessous de 0 °C.

Elle dépend directement de la pluie. Une relation exponentielle existe entre la quantité de pluie tombée et le nombre d'individus capturés, tant pour l'ensemble des espèces capturées que pour les deux espèces les plus communes, *Entomobrya nivalis* et *Orchesella cincta*.

Des bandelettes adhésives placées sur les troncs d'arbre ont montré que l'ascension des Collembolles atteint au moins 5 m. A ce niveau leur abondance vaut environ un cinquième des abondances à 1 et 2 m du sol où elles sont à peu près égales.

Aucune explication satisfaisante ne peut être avancée pour justifier cette fréquente et importante activité. Des changements de concentration gazeuse dans la litière ou la compression après la pluie peuvent occasionner l'abandon des feuilles de litière mais n'expliquent pas l'ascension. La distribution aérienne peut se trouver accrue, mais ceci ne concerne pas des espèces normalement arboricoles telles *Isotoma arborea* qui, comme nous l'avons montré, doivent se trouver occasionnellement en grand nombre sur le sol.

Nous insistons sur le fait que l'usage de «pitfall traps» ne mettra pas en évidence ces vastes mouvements ascensionnels à partir du sol. Par conséquent des techniques complémentaires tels des pièges à eau, à adhésifs ou à aspiration, utilisés au-dessus du niveau du sol, sont essentiels pour mener correctement l'étude des changements d'activité, d'abondance et de distribution des Collembolles.

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7. References

- BERLAND, L., 1934. Etude en avion de la faune entomologique aérienne. C. R. Acad. Sci., Seance 18 Juin, 2201—2203.
 — 1935. Premiers résultats de mes recherches en avion sur la faune et la flore atmosphériques. Ann. Soc. ent. France **104**, 73—96.
 — 1936. L'exploration biologique de l'atmosphère en avion et l'emploi possible de cette méthode en météorologie. La Météorologie **1**, 28—35.
 BUAHIN, G. K. A., 1965. The problems of soil recolonisation by microarthropods. Ph. D. Thesis, Univ. of London. 192 pp.
 CHRISTIANSEN, K., 1964. Bionomics of Collembola. Ann. Rev. Ent. **9**, 147—178.
 DELAMARE-DEBOUTTEVILLE, C., 1951. Microfaune du sol des pays tempérés et tropicaux. Vie et Milieu, Suppl. **1**, 360 pp.
 EDWARDS, C. A., and G. W. HEATH, 1963. The role of soil animals in breakdown of leaf material. In: J. DOEKEN and J. VAN DER DRIFT (eds.): Soil organisms, North Holland Publishing Company, Amsterdam, 76—84.
 FREEMAN, J. A., 1952. Occurrence of Collembola in the air. Proc. R. ent. Soc. Lond. A, **27**, 28.
 GLICK, P. A., 1939. The distribution of insects, spiders and mites in the air. Tech. Bull., U.S.D.A., **673**, 150 pp.
 GRIFFITHS, E., and H. F. BIRCH, 1961. Microbial changes in freshly moistened soil. Nature, London, **189**, 424.
 HÖREGOTT, H., 1960. Untersuchungen über die qualitative und quantitative Zusammensetzung der Arthropodenfauna in den Kiefernkrönen. Beitr. Ent. **10**, 891—916.
 JOOSSE, E. N. G., 1965. Pitfall-trapping as a method for studying surface dwelling Collembola. Zeitschr. Morph. Ökol. Tiere **55**, 587—596.
 KEVAN, P. G., and D. K. McE. KEVAN, 1970. Collembola as pollen feeders and flower visitors with observations from the high arctic. Quaest. ent. **6**, 311—326.
 MOURSI, A., 1962. The attractiveness of CO₂ and N₂ to soil arthropods. Pedobiologia **1**, 299—302.
 PEDIGO, L. P., 1970. Activity and local distribution of surface active Collembola (Insecta). I. Woodland populations. Amer. Midland Nat. **83**, 107—118.
 POOLE, T. B., 1961. An ecological study of the Collembola in a coniferous forest soil. Pedobiologia **1**, 113—137.
 SOUTH, A., 1961. The taxonomy of the British species of *Eutombrya*. Trans. R. ent. Soc. Lond. **113**, 387—416.
 TAYLOR, L. R., 1973. Monitor surveying for migrant insect pests. Outlook Agric. **7**, 109—116.
 THURSTON, J. M., 1958. Rept. Rothamsted Exp. Sta. (1957), 94.
 UETZ, G. W., 1974. A method for measuring habitat space of hardwood forest litter arthropods. Environ. Ent. **3**, 313.
 WALLWORK, J., 1970. Ecology of soil animals. London and New York, 283 pp.
 WILLIAMS, C. G., 1948. The Rothamsted light trap. Proc. R. ent. Soc. Lond., A, **23**, 80—85.

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